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RESEARCH ARTICLE

Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research

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Abstract Changes in key drivers (e.g., climate, disturbance regimes and land use) may affect the sustainability of forest landscapes and set the stage for increased tension among competing ecosystem services. We addressed two questions about a suite of supporting, regulating and provisioning ecosystem services in each of two well-studied forest landscapes in the western US: (1) How might the provision of ecosystem services change in the future given anticipated trajectories of climate, disturbance regimes, and land use? (2) What is the role of spatial heterogeneity in sustaining future ecosystem services? We determined that future changes in each region are likely to be distinct, but spatial heterogeneity (e.g., the amount and arrangement of surviving forest patches or legacy trees after disturbance) will be important in both landscapes for sustaining forest regeneration, primary production, carbon storage, natural hazard regulation, insect and pathogen regulation, timber production and wildlife habitat. The paper closes by highlighting five general priorities for future research. The science of landscape ecology has much to contribute toward understanding ecosystem services and how land management can enhance—or threaten—the sustainability of ecosystem services in changing landscapes.

Keywords Sustainability · Resilience · Greater Yellowstone ecosystem · Pacific Northwest · Climate change · *Pinus contorta* · *Pseudotsuga menziesii* · Fire · Bark beetles · Land use

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Introduction

Many forested landscapes are changing rapidly in response to changes in key social and ecological drivers. Warming climate is altering forest productivity (e.g., Boisvenue and Running 2006; Huang et al. 2010) and the distribution of some tree species (e.g., Schrag et al. 2008; Lenoir et al. 2009, 2010). Climate-induced changes in forest fire regimes and insect outbreaks have been detected (Westerling et al. 2006; Bentz et al. 2010; Wotton et al. 2010), and future climate projections suggest that disturbance regimes could change profoundly in coming decades (Flannigan et al. 2009; Wotton et al. 2010; Westerling et al. 2011). Change in land use is also ongoing. Forest harvesting continues in many landscapes while slowing in others, and exurban development—and thus the extent of wildland-urban interface (Radeloff et al. 2005)—has increased, especially in forested

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landscapes with abundant environmental amenities (e.g., Gude et al. 2006). Collectively, changing drivers will alter landscape heterogeneity and likely set the stage for increased tension among competing ecosystem services (Johnstone et al. 2010; Turner 2010).

A pressing current need is to understand how concurrent changes in climate, disturbance regimes and land use will affect the resilience of forested landscapes and the sustainability of ecosystem services. By *resilience,* we mean the capacity of a system to tolerate disturbance without shifting to a qualitatively different state that is controlled by a different set of processes (Resilience Alliance 2012); i.e., the ability of a system to retain its function, structure, identity and feedbacks in the face of disturbance and environmental change (Walker et al. 2004). By *sustainability*, we mean use of the environment and resources to meet current needs without compromising the ability of system to provide for future generations; here, we deal specifically with the capacity of the system to deliver desired ecosystem services in the face of human land use and a fluctuating environment, now and in the future (Chapin et al. 2010).

Assessing, projecting and managing the flows of ecosystem services across spatially heterogeneous landscapes remain key challenges in sustainability science (e.g., Carpenter et al. 2009). *Ecosystem services* are the benefits people obtain from ecosystems (Daily 1997; Daily et al. 2000; Millenium Ecosystem Assessment [MEA] 2005), and they are increasingly included in policy decisions related to sustainability (National Research Council 2005; Daily and Matson 2008; Carpenter et al. 2009; Daily et al. 2009). Several government programs in the USA (e.g., Environmental Protection Agency and US Department of Agriculture) and in Europe now focus on management of ecosystem services (e.g., Schröter et al. 2005). Categories of ecosystem services are recognized (supporting, regulating, provisioning and cultural; Millennium Ecosystem Assessment 2005), and some sets of ecosystem services called *bundles*—repeatedly appear together across space or time (Raudsepp-Hearne et al. 2010).

Anticipating future flows of ecosystem services is daunting not only because the tempo of change is accelerating for many key drivers, but also because ecosystem services may interact in unexpected ways. *Synergies* occur when multiple services respond to the same drivers of change, or production of one ecosystem service enhances production of another (Bennett et al. 2009; Raudsepp-Hearne et al. 2010). *Tradeoffs* occur when the provision of one service is reduced by increased use of another (Rodriguez et al. 2006). Sometimes tradeoffs result from direct interactions (e.g., forest harvest reduces on-site carbon storage directly; Hudiburg et al. 2009); in other cases, tradeoffs may arise from spatial incompatibilities and/or societal feedbacks (e.g., people may avoid living near a clearcut forest site) (Raudsepp-Hearne et al. 2010). While some tradeoffs reflect explicit choices, others arise without intent or even awareness that they are taking place.

That landscape heterogeneity has myriad influences on population dynamics, community structure, and ecosystem processes is well known. Composition and configuration affect the presence and abundance of species (e.g., Newton et al. 2008, Prugh et al. 2008), the composition of biotic communities (e.g., Dormann et al. 2007), a variety of species interactions (e.g., Hebblewhite et al. 2005), and ecosystem processes ranging from nutrient loading to surface waters (e.g., Strayer et al. 2003) to nutrient retention in terrestrial landscapes (e.g., Bennett et al. 2005). Such strong relationships between landscape heterogeneity and ecosystem structure and function imply that spatial heterogeneity will affect the sustainability of ecosystem services, and thus landscape ecology can make key contributions to sustainability science (e.g., Musacchio 2009; Cumming 2011). However, the role of landscape heterogeneity in the provisioning of ecosystem services or in amplifying or dampening changes in ecosystem services has received little attention.

In this paper, we explore how selected ecosystem services that represent supporting, regulating and provisioning services may change in coming decades, with particular attention to the role of spatial heterogeneity in forested landscapes (Table 1). Using a place-based, regional approach (Musacchio 2009) to provide tangible context, we focus on two contrasting, well-studied landscapes representative of broad swaths of the western US: the Greater Yellowstone Ecosystem (GYE) (northwestern Wyoming, USA), a continental-interior forested landscape, and the coastal temperate rainforest region of the Pacific Northwest (PNW) (western Oregon and Washington, USA). For each region we address two questions: (1) How might the provision of ecosystem services change in the future

Table 1 Ecosystem services and potential trajectories of change in two contrasting forested landscapes of the western US

Ecosystem service	Potential trajectories of change by region				
	Greater Yellowstone ecosystem	Maritime Pacific Northwest	Possible thresholds?	Spatial heterogeneity important?	Key references
Supporting services					
Forest regeneration	Expected to decline at lower treeline and to increase at upper treeline with warming climate; could be reduced substantially by multiple, frequent fires; little influence of land use	Widespread changes not generally expected, with possible exception of the low elevations ecotonal to savanna/woodland vegetation in valley bottoms; reduced snowpack and longer dry season could reduce tree seedling survivorship.	Warming climate plus frequent fire could preclude tree regeneration in some locations in the GYE, producing a shift from forest to nonforest vegetation; similar thresholds in the maritime PNW, if they exist, may require more warming and may not be exceeded until much later.	YES. Amount and configuration of undisturbed patches and individual "legacy" trees that survived prior disturbance, will be important as seed sources for forest regeneration; biophysical gradients will also be important	Powell and Hansen (2007); Littell et al. (2008, 2009, 2010); Donato et al. (2009a, b); Romme et al. (2011); Waring et al. (2011); Westerling et al. (2011)
Primary production	Could increase in warmer climate, because temperature can be limiting; would increase with more young forest cover but decrease if fire frequency and/or drought stress reduced tree cover; land use unlikely to have a large influence	Large changes less likely to result from warming climate alone because productivity is limited more by land use patterns (e.g., forest management) than climate change of the magnitude predicted; exurban development and associated loss of forest land could reduce primary production	Potential conversion of forest to nonforest given warming climate and frequent fire in the GYE, but unlikely for most of maritime PNW.	YES, but indirectly as a function of forest regeneration (see above)	Littell et al. (2008); Hudiburg et al. (2009); Smithwick et al. (2009); Turner et al. (2011)
Regulating services					
Carbon storage (climate regulation)	Trends should closely follow primary production, but carbon storage may be reduced rapidly if two or more disturbances occur in rapid succession. Comment—Two fires in rapid succession would reduce carbon storage, but I'm not sure that MPB outbreaks reduce carbon storage. Maybe restrict this sentence to short-interval fire	Possibility of reduced C storage with increased wildfire activity due to intensified dry seasons late in 21st century; however climate-driven changes in C storage are unlikely to overtake the dominant effect of land-use patterns (forest age). Recent trends in forest management (reduced timber harvest rate) have significantly increased C storage in this highly productive, high-inertia system.	Potential shift from a net C sink to a net C source in the GYE if forests are converted to nonforest given warming climate and frequent fire; this is much less likely in the PNW where disturbance regimes will likely not be as sensitive.	YES, but indirectly as a function of forest regeneration (see above)	Gower (2003); Hudiburg et al. (2009); Smithwick et al. (2009); Turner et al. (2011); Rogers et al. (2011); Kashian et al. (in press)

Table 1 continued

Ecosystem service	Potential trajectories of change by region				
	Greater Yellowstone ecosystem	Maritime Pacific Northwest	Possible thresholds?	Spatial heterogeneity important?	Key references
Natural hazard regulation	Warming climate likely to cause substantial increase in frequency of large fires; the likelihood of damage to human life, property or values if fire occurs increases with exurban development.	Increases in area burned possible but likely not as large, or soon, as interior forest regions. Fire hazard increases with WUI extent. Increased likelihood of extreme precipitation/flood events during winter, with magnitude and impacts tied to land use via the portion of landscape covered in mature forest (interception and moderation of rain-on-snow events).	Spatially heterogeneous fuel conditions and natural fire breaks tend to constrain fire spread and severity under moderate weather conditions, but there are thresholds in fuel moisture and wind speed beyond which weather conditions dominate fire behavior and spatial patterns in fuels are no longer important. Whether (and to what extent) such thresholds are more likely exceeded under future climate trajectories is an active area of research.	YES. Fire hazard depends, in part, on spatial patterns of development (especially WUI). Timber harvest or forest thinning may decrease subsequent fire hazard under moderate burning conditions, depending on types and spatial patterns of harvest.	Hammer et al. (2007); Littell et al. (2009); Turner (2010); Westerling et al. (2011)
Insect and pathogen regulation	Warming climate likely to cause more frequent and extensive bark beetle outbreaks. Outbreaks reduce canopy fuels and may thus reduce severity of subsequent fires in some forest types even as fire frequency increases.	Drought stress and associated vulnerability to bark beetles is less likely than in the GYE. Increased susceptibility to some pathogens may primarily affect lower, drier areas and where forest composition and age structure has been simplified. Changes in root, stem and foliage pathogens depend strongly on subregional variations in seasonality of temperature/moisture.	Warming climate plus land use promoting even-aged, even-sized trees will likely lead to widespread and synchronized insect outbreaks or susceptibility to forest and pathogens. Critical land use effect is introduction of non-native insects and pathogens, which can produce novel system behavior.	YES (linked disturbances). For example, spatial heterogeneity in stand ages and structures following fire creates complex template of suitable hosts for bark beetles, while spatial heterogeneity of bark beetle outbreaks creates complex patterns of fuel that influence behavior and severity of future fires. Spatial variability in postfire stand density/structure may dampen subsequent bark beetle outbreaks because trees reach susceptible size at different times; intensive forest management with even-aged, even-sized trees may increase vulnerability of forests to certain insects and pathogens.	Raffa et al. (2008), Littell et al. (2010), Shaw et al. (2011), Simard et al. (2011)

Table 1 continued

Ecosystem service	Potential trajectories of change by region				
	Greater Yellowstone ecosystem	Maritime Pacific Northwest	Possible thresholds?	Spatial heterogeneity important?	Key references
Provisioning services					
Timber	Difficult to predict: timber production could increase if tree growth is enhanced by warmer climate, but increased frequency and extent of fires or bark beetle outbreaks, or failures of tree regeneration, could reduce timber production	Negligible to slight increases in productivity resulting from warmer climate conditions; outputs are largely dependent on land management regimes. Because climate-induced changes to fire regimes will be minor or later relative to inland regions, disturbance impacts on timber production may be comparatively minor	Thresholds in temperature and precipitation may exist beyond which tree growth and tree regeneration are significantly impaired; these thresholds are not well characterized at present.	YES. Tree growth responds to spatial variation in soils and microclimate, and tree regeneration after disturbance or harvest is influenced by spatial patterns as described above. Maintaining heterogeneity perpetuates a wider variety of silvicultural options for timber management under changing conditions.	Kohm and Franklin (1997); Chhin et al. (2008a, b); Nakawatase and Peterson (2006); Smithwick et al. (2009); Littell et al. (2010)
Wildlife habitat	Habitat for species associated with high-elevation forests (e.g., whitebark pine, subalpine fir, Engelmann spruce), old forests, and riparian zones likely to decline with warmer climate, more frequent fire and increased development. Habitat for species associated with low-elevation forests and grasslands (e.g., aspen, interior Douglas-fir) may increase with climate warming; and younger forests likely to increase.	Redistribution of dominant forest tree species is not likely to be substantial. If snowpack is reduced along with temperature increase, modest potential for adverse effects on salmonid species due to warmer stream temperatures; this will interact with land use activities which affect amount of riparian forest cover and shade. Forest fragmentation is significant and may affect ability of species to persist and migrate.	The potential loss of whitebark pine from the GYE because of climate warming and increased disturbance would be loss of a keystone habitat for grizzly bears and Clark's nutcracker; in the PNW, fragmentation from forest harvest patterns may compromise the ability of some species (e.g., …) to shift geographically in response to changing climate	YES. The composition and configuration of different habitats on the landscape will determine the abundance of wildlife populations; in the GYE, exurban development is particularly affecting riparian habitat, bird hotspots (especially neotropical migrants) and corridors. Habitat fragmentation (from land use or harvesting) will influence species dispersal and migration patterns.	Gallant et al. (2003); Gude et al. (2007); Littell et al. (2009)

given anticipated trajectories of climate, disturbance regimes, and land use? (2) What is the role of spatial heterogeneity in sustaining future ecosystem services? We then conclude by identifying priorities for future research on sustainability of landscapes in general, emphasizing how the science of landscape ecology can contribute to this growing field.

Ecosystem services in changing forest landscapes

The focal regions

The GYE is centered on Yellowstone National Park and encompasses nearly 80,000 km^2 in northwestern Wyoming, Montana and Idaho. Pre-Columbian flora and fauna are largely intact, and fire and vegetation dynamics have been well-studied (Romme and Despain 1989, Whitlock et al. 2008). About 60 % of the GYE is forested, dominated by conifers (e.g., *Pinus contorta* var. *latifolia*, *Picea engelmannii, Abies lasiocarpa, P. albicaulis, Pseudotsuga menziesii*). Fire-return intervals have varied from approximately 100–300 years throughout the Holocene and are largely driven by climate (Whitlock et al. 2003, 2008; Millspaugh et al. 2004); vegetation feedbacks (i.e., fuel controls) have played a lesser role (Millspaugh et al. 2000; Higuera et al. 2010). Native bark beetles are also a key element of this system (Furniss and Renkin 2003), with extensive outbreaks since the 2000s (Simard et al. 2012). Recent studies suggest that spring-summer temperatures may be 4.5–5.5 °C warmer by mid-century, and the fire rotation (i.e., time required to burn the area equivalent to a focal landscape) may decrease to <30 years (Westerling et al. 2011).

The GYE is largely undeveloped (Fig. 1a), but land use is still important. Forest harvesting on the national forests during the mid 20th Century led to a patchwork mosaic of small, dispersed clearcuts in some areas (Tinker et al. 2003). Rates of forest harvest declined in recent years, but exurban development has increased along with a small but expanding population. Between 1970 and 1999, the GYE experienced a 58 % increase in population, and between 1950 and 1999, the number of rural homes in sections bordering public lands increased from 9942 to 39,944 homes (Gude et al. 2006). Development has been concentrated in areas that border the public lands and also on highly productive soils and lands near water, leading to a disproportionate impact on riparian corridors (Gude et al. 2006). Exurban development is expected to increase with changing demographics (Gude et al. 2006, 2007; Hammer et al. 2009), but extensive portions of the GYE remain federally protected wildlands.

The maritime PNW region is west of the Cascade Mountain crest, covering $\sim$150,000 km^2 in western Oregon and Washington. Fire and vegetation dynamics of the region are well documented (e.g., Franklin and Dyrness 1988; Agee 1993). About 70 % of the PNW is covered by maritime temperate rainforests, with montane areas dominated by *P. menziesii*, *Tsuga heterophylla*, *A. procera*, *A. amabils*, and *A. lasiocarpa* and coastal forests dominated by *P. sitchensis* and *T. heterophylla*. Conifer forests have dominated throughout the Holocene (Waring and Franklin 1979; Long et al. 2007; Walsh et al. 2010). Long disturbance intervals and a mild, moist climate support high-productivity, high-biomass forests composed of exceptionally large old trees, which historically covered much of the region (Waring and Franklin 1979; Spies et al. 2007). Fire regimes are climate-driven (not fuel limited), with large stand-replacing fires occurring during rare conditions of extreme drought at 200–500 year intervals, as well as some mixed-severity regimes (Morrison and Swanson 1990; Agee 1993; Weisberg and Swanson 2003; Halofsky et al. 2011). Temperatures are projected to warm in the next century, but the forests west of the Cascade Mountain crest are expected to remain relatively moist (Littell et al. 2010). Wildfire activity may increase (Rogers et al. 2011), and bark beetles may shift upward in elevation (Littell et al. 2010).

Land use and ownership in the PNW is mixed, with $\sim$80,000 km^2 of federal lands primarily in the mountain ranges (Thomas et al. 2006), and privately owned, agricultural and urban areas in the lowlands. Extensive timber harvesting began in the 1800 s, accelerating following World War II with an emphasis on dispersed-patch clearcut silviculture. Over ensuing decades the landscape shifted from dominance by mature/old-growth forests to a patchwork with increasing representation of intensively managed young stands ($\sim$70 % of area, compared to historic levels of $\sim$20 %; e.g., Spies et al. 2007) (Fig. 1b). By the 1990s, however, federal land management goals shifted to conserving biodiversity (e.g., the Northern Spotted Owl, *Strix occidentalis caurina*) (Thomas et al. 2006). Timber harvest and conversion of old-growth forests decreased

Fig. 1 **a** Large portions of the Greater Yellowstone Ecosystem are federally protected wildlands that are subject to natural disturbance regimes including wildfire and bark beetles, both of which may be altered by climate change (Photo by M. G. Turner). **b** Extensive areas of the forested maritime Pacific Northwest have been harvested, creating a patchwork mosaic of managed and unmanaged forests of varying age (Photo by B. E. Law)

precipitously and has remained low on public lands, but short-rotation timber crops remain dominant on private forestlands. In addition, the major population centers for Oregon and Washington are in the region; population increased by 13 % in the last decade (US Census Bureau data), and suburban and exurban development are expanding into forested areas.

Ecosystem services

Ecosystem services are expected to change in the GYE and PNW, but the magnitude of change and relative importance of key drivers-climate, disturbance and land use–are likely to differ between regions (Table 1). The GYE is much drier than the maritime

PNW, and ecosystem services in the GYE are expected to be more sensitive to projected climate change. Although a warming climate could potentially increase net primary production and carbon storage because tree growth is partly limited by cold temperatures and a short growing season in the GYE, any decrease in effective precipitation could limit the growth response to warmer temperatures. Moreover, the frequency and extent of large fires may increase substantially (Westerling et al. 2011). The interaction of warmer, drier climate and frequent fire could compromise tree regeneration and shift portions of the GYE landscape from forest to nonforest, thus reducing all ecosystem services dependent on forest cover (Table 1; Westerling et al. 2011). In contrast, the moist maritime conditions of the PNW provide some inertia that could buffer the effects of climate warming on forests relative to drier inland systems (Littell et al. 2010; Waring et al. 2011). Climate-driven large-scale shifts from forest to nonforest are therefore unlikely in the maritime PNW. However, forest management and exurban development in the PNW affect forest area and age-class distributions and are a dominant influence on ecosystem service production (Table 1). In both regions, future trajectories of ecosystem services will be influenced by interactions among key drivers, which may themselves interact with and/or create landscape patterns. Therefore, anticipating future conditions is not straightforward.

Supporting services

Forest regeneration after natural or human disturbance underpins many ecosystem services and may well be a keystone process. In the GYE, forest regeneration may be impaired by both warming climate and increased fire frequency, though land use will likely have less influence because most of the area is wilderness. In the PNW, however, moist conditions may mediate the effects of warming temperatures on tree regeneration following disturbance (Table 1), but patterns and intensity of timber harvesting and other land uses will be very important. In anticipation of impacts from climate change, thresholds in temperature and precipitation likely exist beyond which tree regeneration and growth are significantly impaired in both regions; these thresholds are not well characterized at present but are the focus of ongoing climate research (e.g., Coops and Waring 2011). In any event, the impacts of climate change and land use on forest regeneration will be spatially heterogeneous; e.g., the earliest manifestations of climate limitations on tree re-establishment will likely be seen on drier microsites (e.g., south-facing aspects near lower timberline), while forests may continue to regenerate on more mesic sites nearby. It would be especially valuable to quantify and map landscape patterns of forest regeneration, as these could identify "hot spots" of other ecosystem services or locations where thresholds might be exceeded in the future (Littell et al. 2010).

Landscape heterogeneity is important for tree regeneration in the GYE and PNW and thus also key for sustainability of an array of ecosystem services, including primary production, carbon storage, timber production and wildlife habitat (Table 1). Even for tree species with an abundant canopy seedbank (e.g., *P. contorta*), spatial variation in fire severity contributes to landscape variation in postfire stand structure, and stands with high postfire tree density accumulate carbon much more rapidly than areas of low-density trees (Turner et al. 2004; Turner 2010). For tree species that lack a canopy seedbank (e.g., *P. engelmannii*, *A. lasiocarpa*, *P. menziesii*), spatial heterogeneity is even more critical because tree regeneration depends on nearby seed sources (Fig. 2a). Thus, the presence of unburned forest patches within a fire, the survival of individual "legacy" trees, and the complex shapes of many natural fires enhance tree regeneration. For example, in locations where the 2002 Biscuit Fire in Oregon re-burned a 15-year-old postfire forest, the legacy trees provided the seed source for tree regeneration (Fig. 2b; Donato et al. 2009a, b). Even in species bearing serotinous cones (e.g., *P. contorta*), legacy trees may create an important on-site seed source for tree regeneration following a short-interval fire. For example, in a short-interval fire in 2007 that reburned areas that burned in the 1988 fires, nearby mature legacy trees appeared to augment local seed supply (*personal observations*). More generally, it is necessary to understand the amount and kinds of heterogeneity that must be maintained to ensure forest regeneration following disturbances in forests that differ in regeneration mechanisms of the dominant tree species.

Because primary production in forested landscapes is dominated by tree production (Campbell et al. 2004), spatial heterogeneity will influence future patterns of primary production via its strong effect

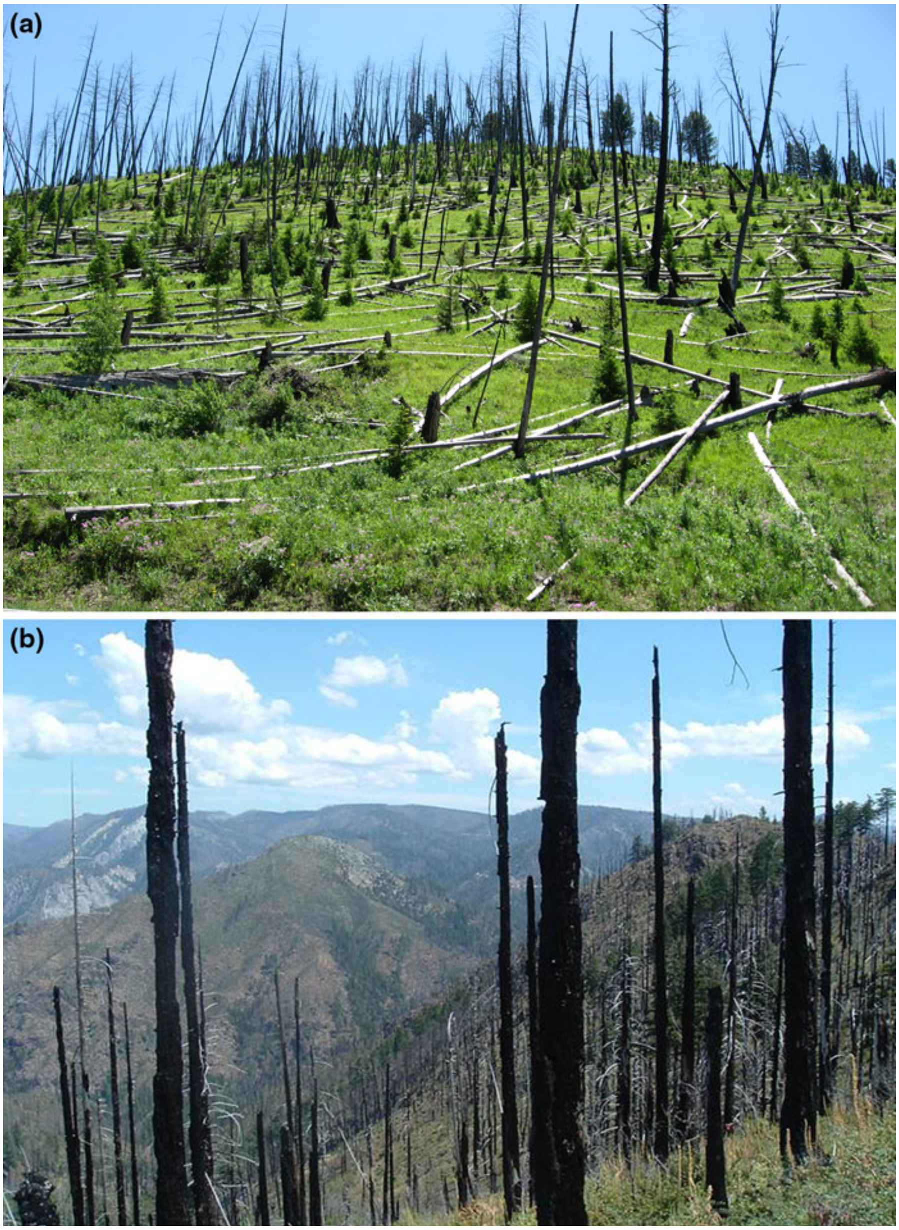

Fig. 2 **a** Following the 1988 Yellowstone fires, surviving legacy trees at the top of the ridge were the likely seed source for these post-fire Douglas-fir trees (Photo from 2011 by M. G. Turner). **b** A Douglas-fir dominated forest that experienced two stand-replacing fires within a short-interval (1987 Silver and 2002 Biscuit Fires in southwest Oregon); scattered patches of legacy mature trees survived both fires and provided important seed sources for regeneration (Photo from 2005 by D. C. Donato)

on forest regeneration (Table 1). Thus, because primary production is such a key supporting service, understanding the importance of spatial heterogeneity for tree regeneration is among the most important priorities for research in forested landscapes.

Regulating services

Among regulating services, carbon storage will depend strongly on rates of primary production and forest regeneration, as discussed above. However, these three services illustrate the potential for ecosystem services that are likely to exhibit synergies over the long term, but nonetheless vary in their short-term responses to changing drivers. Carbon storage should be positively correlated with tree regeneration and net primary production over successional time (100–300 years). However, a reduced interval between successive fires may have an immediate negative impact on ecosystem carbon storage but little initial effect on tree regeneration. For example, in a 2009 fire in the GYE that burned a 28-year-old *P. contorta* forest that had previously regenerated following a stand-replacing fire in 1981, tree regeneration was abundant, ranging from 4,000 to 25,000 stems ha^{-1} (Turner, Romme and Donato, unpublished data). These tree seedling densities are typical of postfire regeneration measured following fires in older forests (e.g., Schoennagel et al. 2003). However, trees killed by the 1981 fire had fallen to the forest floor, and much of those large, woody surface fuels were consumed in the 2009 fire. The short-interval fire reduced postfire carbon storage in downed wood by $\sim$57 % relative to postfire sites that were >150-years-old at the time of burning (Turner, Romme and Donato, unpublished data).

The regulation of natural hazards, especially large wildfires, is of increasing concern throughout the west and in the GYE and PNW (Table 1). Large fires are not inherently catastrophic for forests in either of these two regions, where fires were historically large and severe, and where the biota are adapted to fires of this kind (Agee 1993; Romme et al. 2011). However, in some forests in which historical fires were frequent and low severity, such as southwestern ponderosa pine (*P. ponderosa*), fuel structures have been altered by a century of fire exclusion; large fires in these forests may burn with uncharacteristic severity and unusual damage to the biota (Strom and Fulé 2007). Regardless of forest type and natural fire regime, buildings and infrastructure become increasingly vulnerable to fire damage as human communities and infrastructure expand into fire-prone areas and the climate conditions conducive to large fires become more common (Theobald and Romme 2007).

Wildfire is strongly influenced by landscape heterogeneity (e.g., the abundance and connectivity of fuel, the presence of natural fire breaks, and topographic variability) when fire weather is not extreme. Sound landscape planning can reduce hazards to homes and other structures by placing them in locations where fire spread and severity are inherently lower under most weather conditions (e.g., within areas having lower fuel accumulations) and staying out of especially hazardous locations (e.g., on slopes or draws facing the prevailing wind direction and covered by heavy timber). Strategic placement of timber harvest units or thinning of dense forests also can alter fire behavior and reduce vulnerability of homes and infrastructure (Finney 2001). However, there is little effect of landscape heterogeneity on fire spread or severity when conditions are exceptionally dry and windy; at these times almost any place in the landscape can burn (Turner and Romme 1994). Understanding anticipated trajectories of land use and climate change in each region is necessary to reduce vulnerability to natural hazards in the GYE and PNW landscapes and to understand the degree to which landscape pattern can be managed to enhance resilience to natural hazards.

Forest insects and pathogens also respond strongly to climate drivers in both regions (Table 1), and regulation of their impacts in the future is uncertain. Fire frequency and extent of bark beetle activity both increase with drought and warmer temperatures. However, feedbacks between beetles and fire can be disrupted or enhanced by landscape management, and spatial heterogeneity plays a role in regulating insects and pathogens. The historical fire regime in some forests probably dampened the severity or extent of bark beetle outbreaks, because the trees in younger postfire forests are too small to support a bark beetle outbreak. Outbreaks thus were limited to patches of older forest, especially when surrounded by a matrix of younger forests. However, where fire exclusion or extensive even-aged timber management have produced contiguous areas of forests of similar age and structure, an outbreak beginning in one area can readily spread throughout a region (Raffa et al. 2008). Maintenance or restoration of a natural fire regime, or a timber harvest program that emulates the natural disturbance regime (e.g., Cissel et al. 1999), can enhance regulating services. However, given the magnitude of the projected changes in key drivers (e.g., climate warming), the degree to which our understanding of past landscape dynamics can inform the future is unknown.

Provisioning services

Several key provisioning services—including production of timber and wildlife habitat—depend strongly on supporting services and future drivers. Thus, there are important synergies between timber production and the supporting services of forest regeneration and primary production: all increase as temperature increases, if other factors like moisture or increased fire frequency are not limiting (Table 1). If tree regeneration fails, however, timber production will clearly be reduced where natural (versus planted) regeneration is relied upon for forest restocking. Tree growth also responds to landscape heterogeneity, notably the natural spatial variation in soils and microclimate, and tree regeneration after disturbance or harvest can be enhanced or impaired by management-influenced spatial patterns of biotic legacies such as seed trees, as described above. Further, there are tradeoffs between timber harvest and a key regulating service, namely on-site carbon storage (Hudiburg et al. 2009; Turner et al. 2011), although the net consequences for carbon balance will depend on the fate of the harvested material (Gower 2003). There also may be tradeoffs between timber production and regulation of natural hazards. Larger trees in a forest stand usually are of greatest economic value for timber, but also are typically most fire-resistant; smaller trees and saplings may be the most important components to remove in the interest of reducing fire spread and severity (Agee and Skinner 2005).

Production of wildlife habitat interacts with the other ecosystem services in complex ways (Table 1). There may be synergies between timber production via regeneration harvests (clearcutting) and some species that prefer early-seral habitat, but tradeoffs with species restricted to old-growth forest. Rapid forest regeneration to canopy closure (a supporting service) represents a synergy with closed-forest wildlife habitat, but a tradeoff for early-seral species (Swanson et al. 2011; Donato et al. 2012). Spatial heterogeneity will play particularly important roles for the production of wildlife habitat, with thresholds in habitat quality, habitat connectivity, and/or patch size apparent for many species. For example, the Northern Spotted Owl and pine marten thrive in large patches of old-growth forest but may not persist in patches less than a minimum size (FEMAT 1993). Similarly, species that depend on early-seral habitat may be limited by availability (Fontaine et al. 2009). Because different ecosystem services may interact, it is important to consider the spatial patterns of multiple ecosystem services when evaluating sustainability, and to identify where on the landscape tradeoffs and synergies are most pronounced. Such prospective studies will aid landscape managers by identifying areas of key importance (e.g., hot spots of synergies) as well as locations where conflicts among competing ecosystem services may be pronounced (e.g., hot spots of tradeoffs).

Synthesis

In general, the degree to which landscape patterns can be managed to sustain multiple ecosystem services in the face of other changing drivers is not well understood. Efforts are complicated by synergies and tradeoffs among different services, some of which may be subtle or not yet recognized, and by the inherent spatial variability in ecological characteristics that results from gradients in soils, microclimate, and local history in all landscapes. The interaction of drivers may be the greatest source of complexity and uncertainty. Drivers may interact synergistically or antagonistically, and thus either amplify or dampen consequences, but the potential for synergistic interactions to produce unexpected and undesirable consequences deserves particular attention. For example, as ecological conditions shift across a landscape with climate change, the effects of land use (forest harvest and/or exurban development) and disturbance (fire and insects) may interact with climate to rapidly alter certain key habitats and areas of optimal productivity and carbon storage. Further, different landscapes have unique characteristics and histories and may respond differently to contemporary and future drivers of change (Table 1); thus, comparative studies will be needed. Landscape ecology can make important contributions to understanding the spatial patterns of changing drivers and ecosystem services, identifying when and how spatial heterogeneity can enhance or compromise ecosystem service production, and spatially targeting management interventions.

Landscape ecology, landscape sustainability and priorities for future research

We next highlight five general research questions at the frontier of landscape sustainability science. These emerge, in part, from our consideration of ecosystem services in changing forest landscapes, but we phrase them generally because they can be considered more broadly in other kinds of landscapes.

(1) *What types and levels of spatial heterogeneity contribute to sustained production of ecosystem services and what types and levels do not?* Landscapes are dynamic, all landscapes are unique (Phillips 2007), and there is no optimal landscape mosaic that will increase all ecosystem services. Rather, the composition and configuration of a landscape may enhance or sustain one bundle of ecosystem services and leave others vulnerable to degradation. Understanding the relationships between landscape heterogeneity and the provisioning of ecosystem services within different kinds of landscapes is the foundation from which tradeoffs, synergies, trajectories and management alternatives can be considered. How are the types and amounts of spatial heterogeneity that promote sustainability to be defined? If maintaining a set of ecosystem services within set bounds is desired, what kinds of alternative patterns promote those levels of production?

Spatial heterogeneity, in part through its contribution to forest resilience, may allow adaptation to future environmental change and help to sustain some ecosystem services, but humans often re-scale or re-shape natural heterogeneity. Given that habitat fragmentation may either increase or decrease landscape heterogeneity (e.g., through exurban development or forestry), how can land managers determine the types of spatial heterogeneity that will enhance or impede production of different ecosystem services? The science of landscape ecology can help to sort out the consequences of different kinds of spatial heterogeneity, including those that mimic natural patterns, for ecosystem services.

(2) *Where on the landscape do suites of ecosystem services respond similarly or in opposite directions to anticipated changes, and what are the mechanisms behind such synergies and tradeoffs?* Understanding the kind, amount, distribution and patterning of multiple ecosystem services on the landscape is critical for evaluating synergies and tradeoffs among ecosystem services. Prior work that advocated for ecosystem management (e.g., Christensen et al. 1996) and multiple-use forest management (e.g., Kessler et al. 1992) also identified the need for such understanding, although not always spatially. By quantifying and mapping different ecosystem services, "hot spots" of ecosystem services can be readily identified, along with areas where conflicts over provision of differing ecosystem services are likely to occur (Steffen 2009) or thresholds may be exceeded (Raudsepp-Hearne et al. 2010). In forested landscapes, hot spots of ecosystem services often coincide with higher species and functional diversity (Lavorel et al. 2011). Furthermore, managing spatially explicit relationships among different ecosystem services can strengthen landscape resilience, enhance the provision of multiple services, and help avoid catastrophic shifts (i.e., abrupt losses or declines) in ecosystem service production (Bennett et al. 2009). Thus, in prospective studies, the consequences of changing drivers for a variety of different ecosystem services should be evaluated spatially (e.g., Naidoo et al. 2008; Carpenter et al. 2009).

(3) *What are the implications for resilience and vulnerability of ecosystem services of anticipated trajectories of landscape change?* Anticipating landscape changes and how the benefits people derive from a region will be affected by such changes are difficult, but methods from landscape ecology can contribute to addressing this challenge. Landscape ecology offers well-developed methods for projecting alternative landscape patterns probabilistically and for evaluating the consequences of landscape composition and configuration for different responses (e.g., Perry and Enright 2006; Gude et al. 2007; Berland et al. 2011). These methods should be incorporated into studies that explore future scenarios for ecosystem services, and future landscape patterns should be evaluated in concert with changes in other key drivers. Trajectories of change that lead to sustained or enhanced ecosystem services can then be distinguished from those that cause ecosystem services to decline.

(4) *To what degree can landscape pattern be purposefully managed to enhance the resilience of ecosystem services in the face of changing drivers?* This, perhaps, is one of the largest challenges for landscape sustainability—maintaining the capacity for the landscape to produce ecosystem services in the face of change. Just how much leverage can be gained from "smart" management of land use or strategic interventions to alter landscape patterns? Understanding the mechanisms behind synergies and tradeoffs among ecosystem services can help identify ecological leverage points where small management investments can yield substantial benefits (Bennett et al. 2009). But how much can be gained by manipulating landscape patterns, and under what conditions will the magnitude of changes in some drivers overwhelm the importance

of landscape heterogeneity? Landscape managers can intervene in some drivers to sustain ecosystems services (e.g., land use planning can minimize effects on biodiversity) but have little influence on others (e.g., society may have to simply adapt to climate-induced changes in fire regimes). Managers must know when landscape management can and cannot mitigate undesirable changes.

(5) *How well will understanding of past landscape dynamics and ecosystem services inform the future?* For many regions, predicted future conditions differ vastly from past and current conditions. Some studies suggest that "no-analog" communities will develop in the future (Williams and Jackson 2007), and others indicate that disturbance frequency may exceed that documented throughout the Holocene (Westerling et al. 2011). Concepts such as the historical range of variability (HRV) (Keane et al. 2009, Weins et al. in press) provide a baseline characterization of past landscape structure, function, and dynamics, from which we will be able to detect when a given landscape has moved beyond the historical condition as a result of changing climate, disturbance, and land use drivers. However, the historical condition may not be a suitable restoration target if these drivers move landscapes well outside their HRV (Thompson et al. 2009. Will the relationship between future landscape patterns and production of ecosystem services change fundamentally from that of the past? Can approaches from landscape ecology help scientists and managers anticipate or avoid undesirable surprises?

Recommendations and conclusions

Assuring the continued provision of ecosystem services in the face of environmental change—i.e., maintaining functional landscapes—is one of the most pressing challenges in sustainability science and contemporary landscape ecology. Although many questions remain to be answered, there are actions that can be implemented now to maintain ecosystem services. A practical first step, as the examples we have described from the GYE and PNW regions indicate, is to conserve the inherent spatial heterogeneity that characterizes forest landscapes, even (or especially) after disturbances. Following fire, for example, retaining unburned patches and legacy trees (i.e., avoiding the practice of burning these out during fire suppression actions, and thereby destroying key seed sources for forest regeneration) will serve to maintain the natural heterogeneity that provides important insurance in the face of unpredictable change, enhances biodiversity and affords a greater variety of future silvicultural options to address evolving land use objectives and environmental conditions. Second, land planners and resource managers are already striving to reduce the vulnerability of human populations and critical infrastructure to natural hazards such as wildfire, via land use planning and strategic placement of fuels treatments, and insights from landscape ecology could have direct application for such adaptive strategies. Spatial patterns of development and mitigation treatments directly influence the risk of human life and infrastructure to natural hazards, and different landscape patterns can increase or lower the cost of protection. Third, forest landscapes should be strategically monitored to detect early-warning indicators of change, especially in regions where thresholds may be exceeded (e.g., Scheffer et al. 2009). In particular, studies should focus on the size, frequency and severity of multiple disturbance types; the nature and quantity of post-disturbance vegetation; and the dynamics of upper and lower treeline. We hope the perspectives presented here catalyze additional discussion of these ideas, new research designed to contribute to these pressing challenges, and active steps toward enhancing sustainability of the landscapes on which society depends.

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